ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITIES FOR SEVERAL AGRONOMIC CHARACTERS IN SWEET CORN (ZEA MAYS L.)

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN AGRONOMY

MAY 1970

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ACKNOWLEDGMENT

The writer is indebted to the Institute for Student Interchange, East-West Center, for sponsoring his studies at the University of Hawaii.

He also would like to express his gratitude to Dr. S. G. Carmer, Agronomy Statistical Laboratory, University of Illinois, for the computer program of estimating combining abilities in relation to diallel crossing systems.

We certify that we have read this thesis and that in our opinion it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Agronomy.

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INTRODUCTION

Diallel analysis has been widely used in studies on the nature of gene action both in cross-pollinated crops like maize (46,48) and self-pollinated ones like Nicotiana (30). However, the importance of a knowledge of combining ability in evaluating inbred lines for productiveness in single and double cross combinations has been recognized by Richey (51), Richey and Mayer (52), and Hayes and McClelland (19).

One technique used extensively in corn has been to classify parental lines in terms of their ability to combine in hybrid combinations. With this method the resulting total genetic variation is partitioned into the effects of general and specific combining ability. In this context, Sprague and Tatum (59) defined general combining ability as the average performance of a line in hybrid combinations, and as such, general combining ability is recognized as primarily a measure of additive gene action. Specific combining ability describes those instances in which certain hybrid combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved and is regarded as an estimate of the effects of non-additive gene action.

The objective of the study reported here was to examine the type of gene action involved with respect to plant height, ear height, ear length, shank length, ear diameter, cob diameter, kernel depth, weight with husk, weight husked and mid-silking date in single crosses of sweet corn. A second objective was to evaluate the effectiveness of the component approach as a breeding method for the improvement of agronomic traits.

REVIEW OF LITERATURE

Davis (7) made the first suggestion for the use of inbred varietal crosses as a means of testing for general combining ability. Jenkins and Brunson (26) presented extensive evidence that showed the use of inbred-varietal crosses were as reliable method of testing for general combining ability as the average of separate tests with a group of 9 to 12 unrelated inbreds.

Johnson and Hayes (31) and Cowan (6) classified inbreds for general combining ability based upon inbred varietal performance. As the number of inbreds used in each of the studies was small, they were divided, based on the test cross results, into two groups called low and high combiners.

Jenkins (27) studied the general combining ability in test crosses of eight inbreds that had been selfed from one to eight generations. From a study of yields in test crosses he concluded that the general combining ability became fixed early in the breeding process and that further inbreeding had little influence on combining ability. Later Richey (53,54) reanalyzed Jenkin's data. He concluded that the inbreds changed markedly in relative combining ability during the process of selection in self-pollinated lines through the eight generations of inbreeding. That such changes do occur during selection in self-pollinated lines was the conclusion also from the study by Payne and Hayes (50).

Early testing was proposed by Jenkins (27). As used today it is based on two assumptions. First, that there are marked differences in the combining ability among open-pollinated S_0 plants, and second, the

sample selected through the testing of S_0 or S_1 plants should yield more desirable material for further inbreeding than plants selected by visual means alone. The technique of early testing will be given in greater detail later. It consists of selection of individual plants in early generation populations, selfing each and using pollen of each of these selected plants to cross with a tester. Inbreeding may be continued only with lines that are high combiners as determined by test crosses. This study was reviewed here as early testing was one of the techniques used in studies of general combining ability by Green (16).

Green (16) conducted an interesting study of combining ability. In a comparison of all possible single crosses between thirteen selected inbreds, some of which have been used extensively in double crosses, the general combining ability of each was determined from all twelve possible crosses. I 198 and M 14 were considered to have high general combining ability, and KB 397 and Ill. 4226 low general combining ability.

Jones and Singleton (32) found no benefit, as far as combining ability is concerned, in making new selections in the second generation of inbreds of Stowell's Evergreen sweet corn. None of the new hybrids from inbreds selected in the second generation of inbreeding was better than the hybrid made using the original C 63 and C 50 inbreds. Jenkins (28) studied the segregation for yielding ability of inbreds that had been selfed only once when crossed. He found significant differences between lines. These results supported his 1935 conclusions that there are greater possibilities for selection among large numbers of inbred lines than within lines. He also emphasized testing lines for combining

ability in the early generations of inbreeding.

Sprague and Bryan (58) found a significant difference in combining ability for yield after three and four generations of selfing. Differences were larger among F_3 lines. Hence, selection among F_3 families might be more effective than among F_4 lines. These results are different from those of Jenkins (27). It is not surprising to find such a difference in two experiments and the need for more experimental evidence on this subject is emphasized. Before setting forth this evidence, it may be well to review briefly some of the more important researches dealing with characters of the inbred parents that are more or less closely associated with yield of the F_1 hybrids of such inbreds. Proper selection for such characters is an important part of any maize breeding program and must be utilized in conjunction with tests for combining ability of the inbreds.

Nilsson-Leissner (49) and Jorgenson and Brewbaker (33) in two separate experiments, showed, by means of multiple correlations, that length and diameter of ear, number of rows of kernels, height of plants and yield of inbred parents were positively correlated with yield of the F_1 hybrids. Jorgenson and Brewbaker concluded that the "selection of the most vigorous selfed lines for the production of single and double crosses or synthetic varieties is the proper procedure for practical corn breeding." This recommendation was in complete agreement with that of Nilsson-Leissner. Jenkins (25) corroborated these findings for height of plant, length and diameter of ear and yield of inbred ears. In addition, he found the following characters in the inbreds to be positively associated with yield of the F_1 hybrids: date of tasseling

and silking, number of nodes per plant and below ears, and number of ears per plant. Negative association was found for ear shape index (Diameter/Length).

Davis (8) found a high and significant correlation between inbred-variety yields (top crosses) and the yields of the inbred parents in the first two generations of inbreeding ($r = .638 \pm .08$). He concluded that average yield of the first two selfed generations could be safely used for elimination of some of the lines.

Hayes and Johnson (20) studied, for a three year period, correlation between 14 characters in the inbred lines and yield of the inbred-variety crosses. They found that date silked, plant height, ear height, leaf area, pulling resistance, root volume, stalk diameter, total brace roots, tassel index, pollen yield, yield index and ear length showed positive and significant correlation. Since these characters, which make for general vigor of the inbred parent, are positively associated with combining ability of the inbred as measured by the yield of variety-inbred crosses, Hayes and Johnson arrived at the following conclusion: "It would appear that the production of improved inbreds, as measured by the development of the inbreds themselves, will lead, on the average, to the development of higher yielding double crosses." They also studied the combining ability of inbreds secured by the pedigree method of inbreeding first generation hybrids. They found that lines of good combining ability are obtained more frequently from crosses of inbreds that are good combiners than from crosses between inbreds that are low in combining ability. They concluded, therefore, that combining ability is an inherited character.

Matzinger (45) suggested that the ranking of lines for general combining ability can be accomplished most economically through the use of a tester having a broad genetic base. However, he reported a much wider range in acre yields with inbred testers than with single cross or double cross testers, and he pointed out the possibility that test crosses involving the use of an inbred tester may allow more chance for discrimination than if single cross or double cross testers are used.

Jenkins (28) proposed the production of synthetic varieties by a procedure which has come to be known as "recurrent selection for general combining ability." This procedure, which utilizes a broad gene base tester, has been reported effective in improving combining ability for grain yield (40,41,60). Lonnquist and Rumbaugh (42) concluded that the single cross Wf 9 x M 14 was of no value as a tester for general combining ability.

Hull (24) presented arguments favoring overdominance as a partial explanation for heterosis in corn, and recommended that "recurrent selection for specific combining ability" be given a trial. He pointed out that a stable inbred line would be a more effective tester than a single cross in building up a high complementary relation between the tester and the crossbred lot under selection.

McGill and Lonnquist (47) found that 2 cycles of selection for combining ability with Wf 9 x M 14 were effective. Sprague, et al. (62) reported that 2 cycles of selection for combining ability with the inbred line Hy resulted in yield increases of 6.5 bushels per acre in one series and 20.0 bushels per acre in another. Lonnquist and Gardner (43), studying 12 cornbelt varieties and their crosses, reported that general

combining ability effects were more important than the specific combining ability effects.

Horner, et al. (23) indicated that recurrent selection for combining ability with inbred line testers is a more effective method of improving grain yield in corn than recurrent selection for combining ability with a broad base tester. Troyer and Hallauer (63) evaluated a diallel set of 10 early flint varieties of maize for yield and seven other traits at two planting rates and dates. Highest average yields were obtained on the early planting date at high planting rate. Average yields for both dates and rates were 2,536 and 4,167 kg/ha for the 10 varieties and 45 variety crosses, respectively.

Diallel crosses have been utilized extensively to determine the value of the parent in hybrid combinations. The diallel cross appears to have been first proposed by Yates (65). Hayman (21,22), and Jinks (30), and Jinks and Hayman (29) outlined the analysis. Griffing (17) suggested various experimental techniques for studies of combining ability using F_1 progeny with and without reciprocals and parental clones. Littlewood, Carmer, and Hittle (39) developed a computer program for analysis of diallel crosses for the four methods and the two models proposed by Griffing.

Sprague and Tatum (59) presented a method for estimating general and specific combining ability in the yield of single crosses. They pointed out that in a population unselected for combining ability, genes with additive effects (general combining ability) are either more common or produce relatively greater effects than genes with dominance or epistatic effects are more important than genes with additive effects

since the selected lines have a higher degree of similarity in performance than the original population.

East (9) has postulated a hereditary mechanism in corn involving sets of multiple alleles in which certain of the heterozygous genotypes possible at a given locus are superior to any of the possible homozygous genotypes.

Comstock and Robinson (4) presented the theoretical derivation together with an experimental procedure applicable to corn which permits the estimation of the additive and non-additive portions of genetic variance. Rojas and Sprague (57) studied the yields of single crosses involving lines previously selected for general combining ability was consistently greater than the variance may include not only dominance and epistatic variance but also a considerable portion of the genotype-environment interaction variance. Lonnquist and Gardner (43) studied F_1 and F_2 random mating generations from a cross between two corn-belt inbred lines and found that additive genetic variance exceeded dominance variance in all but one of the seven characters involved.

Gray (13,14,15) studied a diallel series of intervarietal crosses in Leucaena leucocephala. It was used to estimate general and specific combining ability for length of main stem and stem number in four varieties of contrasting growth habits. Significant differences were found between varieties for variations due to specific combining ability for length of main stem, but not for stem number. He also obtained measurements on leaf size, stem length, and flowering date on F_2 populations of several crosses for the five varieties of Leucaena

leucocephala. Genotypic effects were significant for each character. Most of the F_1 means approximated to three of the higher parent. The asymmetrical distribution of the F_1 means about the mid-parent point indicated that there was some heterosis, in addition to additive effects. Phenotypic variances for the F_2 population were low in relation to the estimated non-additive genetic variance. In length of main stem 3 months after planting, genetic variance accounted for 21.9 per cent of the total variance, and partition of variation showed the presence of strong non-additive and additive genetic components, and the absence of any non-additive genetic component.

The concept of partitioning the total genotypic variance into various genetic components is due to Fisher (11) and used by him in evaluating covariances between relatives. Fisher also originated the completely generalized genetic model which was later used by Giffing. A model developed by Kempthorne (34) which is adapted to random mating populations and which allows a complete orthogonal partitioning of the total epistatic variance, will be used in the studies reported herein. The estimation of the additive and non-additive genetic components will be made from the experimental material in terms of general and specific combining ability variances.

MATERIALS AND METHODS

At the initiation of the experiment an attempt was made to obtain a representative sample of American sweet corn (Zea mays L.) germ-plasm. Accordingly, the following nine inbred lines (4 Hawaiian and 5 mainland) were chosen.

Inbred lines	Origin
AA 8	Hawaii A 19-6-1-1
AA 11	Hawaii C 5-1-2-3-s1
AA 18	Hawaii B 10-3-3-1-2s
AA 20	Hawaii B 10-4-1-3-1-s1
190a	Illinois 190a: 60cr. H 7B
245	Purdue P 39 x 81-1
2277	Purdue P 51 x Iowa 747
P 39	Purdue Golden Bantam
T 19	Illinois

These nine parents were grown at the Hawaii Agricultural Experiment Station at Waimanalo. Diallel crosses were made in 1968, excluding reciprocals. All 36 crosses were planted at Waimanalo Experiment Station of University of Hawaii on April 3 and June 6 in 1969.

A randomized complete block design with two replications was used at each planting date. Individual plots were single rows containing 30 plants spaced 19 cm apart, with row-spaced 98 cm apart. Seeding rate was three kernels per hill, and stand was thinned to one plant per hill when plants were about 30 cm high.

The Waimanalo soil is a silty clay with pH 6.5. Fertilizer was applied at the rate of 90 lbs N, 39.6 lbs P, and 74.7 lbs K at 600 lbs/acre of triple 15 and later 350 lbs of ammonium sulfate per acre was applied. Weeds were controlled by atrazine applied as a pre-emergence

spray (3 lbs/acre).

Weather records at Waimanalo during the growing season April-September 1969 are summarized as follows.

Month	Total Rainfall (in.)	Max. Temp. (°F)	Min. Temp. (°F)
April	1.60	78.6	67.3
May	2.64	82.7	73.5
June	1.13	85.1	71.7
July	1.89	84.4	74.0
August	0.66	85.6	75.1
September	1.60	84.3	73.8

Ten plants were selected at random in each row and observations were made on ten characters related to productivity, i.e., plant height (cm), ear height (cm), ear length (cm), shank length (cm), ear diameter (cm), cob diameter (cm), kernel depth (cm), weight with husk (kg), weight husked (kg), and mid-silking date (recorded as the number of days from the date of planting until one-half of the plants had silked).

The agronomic traits for the April planting, the June planting, and combined dates were analyzed by a computer program for a randomized complete block analysis obtained from the Department of Agronomy and Soil Science, University of Hawaii. The analysis of the estimates of general and specific combining ability were made according to Griffing (17) method 4, model I and II. These g.c.a. and s.c.a. analyses were made with a computer program according to Littlewood, et al. (39). The computation facilities of the University of Hawaii, Statistical and Computing Center were used for these studies.

Presentation of Analysis

In the randomized-block design we assume that there are 'a' varieties (i.e. the genotypes determined by the diallel crossing method), each of which is assigned at random to each of 'b' blocks, and that there are 'c' individuals in each of the 'ab' plots. Thus the mathematical model for the ijklth observation is assumed to be

$$x_{ijkl} = u + v_{ij} + b_k + (bv)_{ijk} + e_{ijkl}$$

where u is the population mean, v_{ij} is the effect for the ijth genotype, b_k is the kth block effect, $(bv)_{ijk}$ is the interaction between the ijth genotype and the kth block, and e_{ijkl} is the environmental effect peculiar to the ijklth individual. A double subscript notation is used for the variety (i.e. genotypic) effect because it is desired to denote the genotypic means in the combining ability analyses as x_{ij}, where x_{ii} is the mean for the ith parent, and x_{ij} is the mean for the F_1 resulting from crossing the ith and jth parents. In the combining ability analyses, the variety effects are considered in terms of general and specific combining ability effects, such that

$$v_{ij} = g_i + g_j + s_{ij}$$

for those diallel crossing methods in which reciprocal F_1's are not included. In this equation g_i is the general combining ability (denoted as g.c.a.) effect of the ith parent, g_j is the general combining ability effect of the jth parent, and s_{ij} is the specific combining ability (denoted as s.c.a.) effect for the cross between the ith and jth parents.

In this study we wish to present analyses for the two assumptions in which the genotypes are assumed to be (1) a random sample from a population, and (2) a chosen or fixed sample. In the first situation the genotypic effects are considered random variables and in the second they are considered constant. We must now consider how these assumptions are to be integrated with the more general set of assumptions which are made with regard to the elements in the mathematical model for the randomized-block design.

There are two sets of assumptions which can be considered with regard to the variety (genotypic) and block effects. These are (1) the variety and block effects are constants, and (2) the variety and block effects are both random variables.

The first set of assumptions leads to the model in which all effects except the error are regarded as constants. The second set of assumptions leads to a model in which all effects except u are random variables. These two classes of models have been designated as models I and II respectively by Eisenhart (10).

In model I the experimental material is to be regarded as the population about which inferences are to be made. The objectives are to compare combining abilities of the parents when the parents themselves are used as testers, and to identify the higher yielding combinations. Thus we are particularly interested in estimating combining ability effects and computing appropriate standard errors for differences between effects. For the testing procedure it is necessary to assume only that the e_{ijkl} are normally and independently distributed with mean zero and variance σ_e^2.

In model II the assumption is that we are dealing with random samples from some parent population, and the inferences are not to be made about the individual lines in the sample but about the parameters in the parent population. In particular, we are interested in estimating the genetic and environmental components of the complex population variance. To do this we assume that the effects in the model (except u) are normally and independently distributed with mean zero and variances σ_e^2, where θ = b, g, s, or γ. The variance component estimates are then obtained for any given diallel crossing method by equating the observed to the expected mean squares in the appropriate analysis of variance. The standard errors for the variance component estimates are calculated from the variances of the appropriate mean squares. These expectations of mean squares are presented in Table I.

It should be emphasized that the proper interpretation of the combining ability effects and variance depends on the particular diallel method, the assumptions regarding the experimental material, and the conditions imposed on the combining ability effects. For example, when model I is used the equations for estimating the combining ability effects vary from one diallel method to another. These estimators yield unbiased estimates of the combining ability effects only when the specified constraints are imposed on the elements. These constraints vary from one method to another. Finally, valid inferences can be made only about the particular experimental material used. When model II is used, the kinds of inferences which can be made validly will depend on the particular diallel crossing method employed and on the nature of the population from which the lines were drawn.

TABLE I. RANDOMIZED-BLOCK ANALYSIS OF VARIANCE GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODEL I AND II

Source	D.F.	Mean Square*	Expectations of Mean Squares	
			Model I	Model II
Varieties	a-1	M_v	$\sigma_e^2 + bc\phi(v)$	$\sigma_e^2 + c\sigma_{bv}^2 + bc\sigma_v^2$
Blocks	b-1	M_b	$\sigma_e^2 + ac\phi(b)$	$\sigma_e^2 + c\sigma_{bv}^2 + ac\sigma_b^2$
Varieties x blocks	(a-1)(b-1)	M_{bv}	$\sigma_e^2 + c\phi_1(bv)$	$\sigma_e^2 + c\sigma_{bv}^2$
Error	ab(c-1)	M_e	σ_e^2	σ_e^2

*Where

$$\phi(v) = \frac{1}{a-1}\Sigma_i v_i^2; \qquad \phi_1(bv) = \frac{1}{(a-1)(b-1)}\Sigma_{i<j}\Sigma_k (bv)_{ijk}^2;$$

$$\phi(b) = \frac{1}{b-1}\Sigma_k b_k^2;$$

Statistical Analyses

The test for differences among genotypes is made by either of the following F tests. For model I, use

$$F_{[(a-1),\ m]} = M_v/M_e,$$

where (a-1) and m are the degrees of freedom associated with the numerator and denominator of the F ratio, and M_v and M_e are the variety and error mean squares respectively in the randomized-block analysis.

For model II, use

$$F_{[(a-1),\ (a-1)\ (b-1)]} = M_v/M_{bv},$$

where M_{bv} is the variety x block interaction mean square.

If significant F ratios occur we reject the null hypothesis and assume that there are genotypic differences, which may be investigated further with the appropriate combining ability analysis.

Experimental Method

In method 4, the most common of the diallel crossing systems, there are $a = p(p-1)/2$ different F_1 mean values. Method 4 model I and II were used in this analysis.

The combining ability analysis of variance for method 4 model I and II is given in Table II.

TABLE II. ANALYSIS OF VARIANCE FOR METHOD 4 GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODELS I AND II

Source	D.F.	Sum of Squares*	Mean Squares	Expectation of Mean Squares	
				Model I	Model II
General combining ability	p-1	S_g	M_g	$\sigma^2 + (p-2)\frac{1}{p-1}\sum_i g_i^2$	$\sigma^2 + \sigma_s^2 + (p-2)\sigma_g^2$
Specific combining ability	p(p-3)/2	S_s	M_s	$\sigma^2 + \frac{2}{p(p-3)}\sum_{i<j}\sum s_{ij}^2$	$\sigma^2 + \sigma_s^2$
Error	m	S_e	M_e'	σ^2	σ^2

*Where

$$S_g = \frac{1}{p-2}\sum_i X_{i.}^2 - \frac{4}{p(p-2)}X_{..}^2,$$

$$S_s = \sum_{i<j}\sum x_{ij}^2 - \frac{1}{p-2}\sum X_{i.}^2 + \frac{2}{(p-1)(p-2)}X_{..}^2.$$

Model I

The model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{bc}\sum_{k}\sum_{l} e_{ijkl} \qquad \begin{matrix} i,j=1,\ldots,p, \\ k=1,\ldots,b, \\ l=1,\ldots,c, \end{matrix}$$

where u is the population mean, g_i and g_j are the g.c.a. effects, s_{ij} is the s.c.a. effect such that $s_{ij} = s_{ji}$, and e_{ijkl} is the error effect peculiar to the ijklth observation.

The restrictions

$$\sum_{i} g_i = 0,$$

and

$$\sum_{i \neq j} s_{ij} = 0 \text{ (for each j)},$$

are imposed on the combining ability effects.

The expectations of mean squares are given in the column designated model I of Table II. In this analysis

$$M_e' = M_e/bc.$$

Differences within classes of effects are tested by F ratios.

(1) To test g.c.a. effects use

$$F_{[(p-1),m]} = M_g/M_e'.$$

(2) To test s.c.a. effects use

$$F_{[p(p-3)/2,m]} = M_s/M_e' .$$

The effects may be estimated as follows:

$$\hat{u} = \frac{2}{p(p-1)} X_{..},$$

$$\hat{g}_i = \frac{1}{p(p-2)} [pX_{i.} - 2X_{..}],$$

and

$$\hat{s}_{ij} = x_{ij} \frac{1}{p-2} (X_{i.} + X_{j.}) + \frac{2}{(p-1)(p-2)} X_{...}$$

The variance of any F_1 mean value is

$$\text{var}(x_{ij}) = \hat{\sigma}^2 = M'_e,$$

and the variance of a difference between any two mean values is

$$\text{var}(x_{ij} - x_{kl}) = 2\hat{\sigma}^2.$$

Variances of effects and of differences between effects may be estimated as follows:

$$\text{var}(\hat{u}) = \frac{2}{p(p-1)} \hat{\sigma}^2,$$

$$\text{var}(\hat{g}_i) = \frac{p-1}{p(p-2)} \hat{\sigma}^2,$$

$$\text{var}(\hat{s}_{ij}) = \frac{p-3}{P-1} \hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{g}_i - \hat{g}_j) = \frac{2}{p-2} \hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{s}_{ij} - \hat{s}_{ik}) = \frac{2(p-3)}{p-2} \hat{\sigma}^2 \qquad (i \neq j,k;\ j \neq k),$$

$$\text{var}(\hat{s}_{ij}-\hat{s}_{kl}) = \frac{2(p-4)\hat{\sigma}^2}{p-2} \qquad (i\neq j,k,l;\ j\neq k,l;\ k\neq l).$$

Model II

The model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b}\Sigma b_k + \frac{1}{b}\Sigma(bv)_{ijk} + \frac{1}{bc}\Sigma\Sigma e_{ijkl},$$

where all effects except u are random variables.

The expectations of mean squares are given in Table II in the column designated model II. As with other model II analyses

$$E(M'_e) = \frac{1}{bc}(\sigma_e^2+c\sigma_{bv}^2) = \sigma^2.$$

F ratios may be used to test hypotheses pertaining to the variance components:

(1) To test $\sigma_g^2 = 0$ use

$$F_{[(p-1),p(p-3)/2]} = M_g/M_s.$$

(2) To test $\sigma_s^2 = 0$ use

$$F_{[p(p-3)/2,m]} = M_s/M'_e.$$

The variance components are estimated as follows:

$$\hat{\sigma}_g^2 = \frac{1}{p-2}[M_g-M_s],$$

and

$$\hat{\sigma}_s^2 = M_s-M'_e.$$

Approximate estimates of the variances for the variance components may be obtained as follows:

$$\text{var}(\hat{\sigma}_g^2) \simeq \frac{2}{(p-1)(p-2)^2} M_g^2 + \frac{4}{p(p-2)^2(p-3)} M_s^2,$$

$$\text{var}(\hat{\sigma}_s^2) \simeq \frac{4}{p(p-3)} M_s^2 + \frac{2}{m}(M_e')^2,$$

and

$$\text{var}(\hat{\sigma}^2) \simeq \frac{2}{m}(M_e')^2.$$

Griffing described 4 methods using models I and II for the diallel analysis.

Method 1. The parents, one set of F_1's and reciprocal F_1's are included in the analysis.

Method 2. The parents and one set of F_1's, excluding reciprocal F_1's, are included in the analysis.

Method 3. One set of F_1's and reciprocals but not the parents are included in the analysis.

Method 4. One set of F_1's but neither parents nor reciprocal F_1's are included in the analysis.

RESULTS

Components of Variance

Considerable differences among hybrids were found for all agronomic traits (Table III). Mean squares obtained from the randomized-block analyses of variance for hybrids involving the ten agronomic traits of April and June planting and Combined dates revealed that differences among hybrids were highly significant for all the ten traits under consideration (Tables IV and V). Since significant differences among hybrids were found, combining ability analyses were performed. Results are presented in Tables VI, VII, VIII, and IX. As other workers (3,16,18,37,47) have found, general combining ability (denoted as g.c.a.) was the major component of the variation. Specific combining ability (denoted as s.c.a.) was significant for all traits except for plant height of the June planting.

Estimates of the variance components and associated percentage variations for general and specific combining ability for seven traits, based on model I, are presented in the lower part of Tables VI, VII, VIII, and IX. The estimated components of variance for s.c.a. were larger than those of g.c.a. except for plant height, ear height and cob diameter.

Mean squares and components of variance from combining ability analyses, based on model I, of April planting are presented in Table VI. Variation due to g.c.a. and that due to s.c.a. were significant for plant height, ear height, and ear length. Estimated g.c.a. components for the 3 traits plant height, ear height, and ear length accounted for

TABLE III. HYBRID PERFORMANCE FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), EAR LENGTH(X_3), SHANK LENGTH(X_4), EAR DIAMETER(X_5), COB DIAMETER(X_6), KERNEL DEPTH(X_7), WEIGHT WITH HUSK(X_8), WEIGHT HUSKED(X_9), AND MID-SILKING DATE(X_{10}) FOR APRIL AND JUNE PLANTING AND COMBINED DATES

Hybrids	April			June			Combined (A+J)			June						
	(X_1) (cm)	(X_2) (cm)	(X_3) (cm)	(X_1) (cm)	(X_2) (cm)	(X_3) (cm)	(X_1) (cm)	(X_2) (cm)	(X_3) (cm)	(X_4) (cm)	(X_5) (cm)	(X_6) (cm)	(X_7) (cm)	(X_8) (kg)	(X_9) (kg)	(X_{10}) (days)
H X M*																
AA18 X 190a	237	92	16.1	251	77	17.8	244	95	16.9	10.7	4.9	2.4	1.1	3.77	2.64	52
AA18 X 245	261	116	14.8	266	116	17.2	264	116	16.0	11.8	4.5	2.0	1.1	3.23	2.14	51
AA18 X 2277	248	105	14.5	247	89	14.5	247	97	14.5	10.4	4.2	2.0	1.0	2.36	1.73	51
AA18 X P39	254	108	16.4	264	107	15.6	259	107	16.0	12.1	4.4	1.9	1.1	2.91	2.05	50
AA18 X T19	251	107	17.0	264	117	17.2	258	112	17.1	10.4	4.4	2.0	1.0	3.45	2.23	51
AA20 X 190a	233	85	17.8	242	97	16.6	238	91	17.2	8.9	4.8	2.3	1.1	3.68	2.59	54
AA20 X 245	260	112	16.9	265	119	17.7	262	116	17.3	12.5	4.6	2.0	1.1	3.55	2.23	52
AA20 X 2277	240	96	16.3	245	103	15.2	240	100	15.7	11.4	4.5	1.9	1.1	2.77	2.05	50
AA20 X P39	241	103	16.8	256	98	14.7	249	100	15.7	11.1	4.4	2.0	1.0	2.77	1.82	52
AA20 X T19	246	100	17.7	264	109	17.3	255	104	17.5	11.9	4.3	2.0	1.1	3.41	2.14	51
AA8 X 190a	231	88	16.7	240	92	14.9	236	90	15.8	8.1	4.4	2.0	1.0	3.09	2.27	54
AA8 X 245	258	101	14.9	265	109	15.2	261	105	15.1	9.3	4.5	2.0	1.1	2.95	1.86	53
AA8 X 2277	241	95	14.1	235	83	14.1	238	89	14.1	12.0	4.0	1.8	1.0	2.36	1.77	50
AA8 X P39	238	90	14.7	252	96	14.4	245	93	14.6	11.4	4.2	1.8	1.0	2.27	1.50	52
AA8 X T19	242	90	16.2	258	93	15.0	250	91	15.6	11.8	4.0	1.8	1.0	2.73	1.82	50
AA11 X 190a	221	81	17.2	265	109	16.8	243	95	17.0	9.1	4.6	2.1	1.1	3.23	2.14	53
AA11 X 245	261	99	16.5	268	108	15.9	265	104	16.2	11.1	4.4	2.0	1.1	3.00	2.05	53
AA11 X 2277	227	85	14.8	240	91	14.5	234	88	14.6	10.9	4.1	1.7	1.1	2.59	1.91	50
AA11 X P39	226	78	15.7	239	86	14.5	232	82	15.1	12.0	4.2	1.8	1.1	2.59	1.68	52
AA11 X T19	243	99	15.6	266	105	16.1	255	102	15.8	11.3	4.2	1.7	1.0	2.95	2.00	52
Mean	242 (cm)	96 (cm)	16.1 (cm)	254 (cm)	100 (cm)	15.6 (cm)	248 (cm)	98 (cm)	15.9 (cm)	10.9 (cm)	4.4 (cm)	2.0 (cm)	1.1 (cm)	2.98 (kg)	2.01 (kg)	52 (days)
H X H**																
AA8 X AA11	252	117	14.7	273	117	15.7	263	117	15.2	8.9	4.2	1.9	1.0	2.45	1.82	56
AA8 X AA18	248	110	14.5	272	124	15.3	260	117	14.9	8.7	4.2	1.9	1.0	2.73	2.00	56
AA8 X AA20	250	116	16.1	269	121	15.8	259	118	16.0	5.8	4.5	2.1	1.1	2.73	1.95	56
AA11 X AA18	261	127	15.0	276	127	14.9	268	127	14.9	7.6	4.1	1.8	1.0	2.64	1.95	56
AA11 X AA20	242	118	16.0	262	120	15.4	252	119	15.7	10.3	4.4	2.0	1.0	2.77	2.00	56
AA18 X AA20	217	96	12.6	250	120	13.5	234	108	13.1	7.4	4.0	1.9	0.9	1.95	1.23	61
Mean	245 (cm)	114 (cm)	14.8 (cm)	267 (cm)	121 (cm)	15.1 (cm)	256 (cm)	117 (cm)	15.0 (cm)	8.1 (cm)	4.3 (cm)	1.9 (cm)	1.0 (cm)	2.54 (kg)	1.82 (kg)	57 (days)
M X M***																
190a X 245	223	64	15.9	225	67	16.8	224	65	16.3	10.6	4.5	2.1	1.1	3.64	2.18	53
190a X 2277	204	57	17.0	214	60	15.5	209	58	16.3	11.2	4.2	2.1	1.0	2.64	2.05	51
190a X P39	185	47	14.8	213	57	14.1	199	52	14.4	11.8	4.1	2.0	1.0	2.50	1.73	52
190a X T19	215	64	16.2	230	65	15.3	230	64	15.8	13.0	4.4	2.1	1.0	3.09	2.09	51
245 X 2277	212	63	16.1	225	77	15.9	218	70	16.0	10.1	4.1	1.8	1.0	2.82	1.95	51
245 X P39	212	64	13.7	228	69	13.4	220	67	13.5	14.4	4.2	1.8	1.0	2.32	1.36	52
245 X T19	231	76	16.1	236	79	15.8	233	77	15.9	10.0	4.1	1.8	1.0	3.00	1.73	51
2277 X P39	204	70	15.4	209	61	13.5	207	65	14.5	12.7	3.9	1.7	1.0	2.23	1.64	51
2277 X T19	209	63	15.1	219	68	15.2	214	66	15.1	10.5	3.8	1.7	1.0	2.64	1.91	50
P39 X T19	220	57	15.8	219	59	14.2	220	58	15.0	12.4	4.7	2.1	1.0	2.55	1.64	51
Mean	211 (cm)	62 (cm)	15.0 (cm)	222 (cm)	66 (cm)	15.0 (cm)	217 (cm)	64 (cm)	15.3 (cm)	11.7 (cm)	4.2 (cm)	2.0 (cm)	1.0 (cm)	2.74 (kg)	1.82 (kg)	51 (days)
Overall mean	232	91	15.5	248	95	15.3	240	93	15.4	10.3	4.3	2.0	1.1	2.75	1.88	52

**Hawaiian X Hawaiian ***Mainland X Mainland

TABLE IV. OBSERVED MEAN SQUARES FROM RANDOMIZED-BLOCK ANALYSES OF VARIANCE FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), AND EAR LENGTH(X_3) FOR APRIL AND JUNE PLANTING AND COMBINED DATES

Source	D.F.	Mean Square		
		April		
		X_1	X_2	X_3
Hybrids	35	0.727**	0.861**	25.586**
Replication	1	0.650	0.216	66.491
Hybrids x reps	35	0.086	0.047	9.571
Error	648	0.011	0.012	2.695
Source	D.F.	June		
		X_1	X_2	X_3
Hybrids	35	0.812**	0.916**	27.993**
Replication	1	0.003	0.600	6.709
Hybrids x reps	35	0.448	0.042	3.445
Error	648	0.433	0.008	1.267
Source	D.F.	Combined Dates		
		X_1	X_2	X_3
Hybrids	35	1.273**	1.709**	43.556**
Replication	3	3.141	0.543	33.780
Hybrids x reps	105	0.267	0.052	7.680
Error	1296	0.221	0.010	1.981

**P<0.01

TABLE V. OBSERVED MEAN SQUARES FROM RANDOMIZED-BLOCK ANALYSES OF VARIANCE FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), EAR LENGTH(X_3), SHANK LENGTH(X_4), EAR DIAMETER(X_5), COB DIAMETER(X_6), KERNEL DEPTH(X_7), WEIGHT WITH HUSK(X_8), WEIGHT HUSKED(X_9), AND MID-SILKING DATE(X_{10}) OF JUNE PLANTING

		Mean Square		
Source	D.F.	X_1	X_2	X_3
Hybrids	35	0.812**	0.916**	27.993**
Replication	1	0.003	0.600	6.709
Hybrids x reps	35	0.448	0.042	3.445
Error	648	0.433	0.008	1.267
Source	D.F.	X_4	X_5	X_6
Hybrids	35	62.338**	1.176**	0.471**
Replication	1	124.376	0.159	0.561
Hybrids x reps	35	38.216	0.073	0.111
Error	648	11.292	0.033	0.017
Source	D.F.	X_7	X_8	X_9
Hybrids	35	0.063**	0.396**	0.167**
Replication	1	0.007	0.317	0.021
Hybrids x reps	35	0.015	0.012	0.013
Error	648	0.006		
Source	D.F.	X_{10}		
Hybrids	35	0.131**		
Replication	1	0.001		
Hybrids x reps	35	0.011		

**P<0.01

TABLE VI. COMBINING ABILITY MEAN SQUARES AND ESTIMATED VARIANCE COMPONENTS, BASED ON MODEL I, FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), AND EAR LENGTH(X_3) OF APRIL PLANTING

Source	D.F.	Mean Squares		
		X_1	X_2	X_3
General combining ability	8	0.1066**	0.1594**	2.1451**
Specific combining ability	27	0.0155**	0.0085**	1.0216**
Error	648	0.0005	0.0006	0.1347
Components		X_1	X_2	X_3
$\frac{1}{8}\sum_i g_i^2$		0.0152[1] (49.51)[2]	0.0227 (72.52)	0.2872 (21.94)
$\frac{1}{27}\sum_{i<j}\sum s_{ij}^2$		0.0150 (48.86)	0.0080 (25.56)	0.8869 (67.75)
$\hat{\sigma}_e^2$		0.0005 (1.63)	0.0006 (1.92)	0.1348 (10.31)

**P<0.01

1) Estimate of the component.

2) Percent value obtained by the component.

TABLE VII. COMBINING ABILITY MEAN SQUARES AND ESTIMATED VARIANCE COMPONENTS, BASED ON MODEL I, FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), AND EAR LENGTH(X_3) OF JUNE PLANTING

Source	D.F.	Mean Squares		
		X_1	X_2	X_3
General combining ability	8	0.0845**	0.1817**	3.1974**
Specific combining ability	27	0.0275	0.0065**	0.8690**
Error	648	0.0217	0.0004	0.0634
Components		X_1	X_2	X_3
$\frac{1}{8}\sum g_i^2$		0.0090[1] (24.59)[2]	0.0259 (79.94)	0.4477 (34.00)
$\frac{1}{27}\sum\sum_{i<j} s_{ij}^2$		0.0059 (16.12)	0.0061 (18.83)	0.8057 (61.19)
$\hat{\sigma}_e^2$		0.0217 (59.29)	0.0004 (1.23)	0.0634 (4.81)

**P<0.01 1) Estimates of the component.

2) Percent value obtained by the component.

TABLE VIII. COMBINING ABILITY MEAN SQUARES AND ESTIMATED VARIANCE COMPONENTS, BASED ON MODEL I, FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), AND EAR LENGTH(X_3) OF COMBINED DATES

Source	D.F.	Mean Squares		
		X_1	X_2	X_3
General combining ability	8	0.0874**	0.1693**	2.0304**
Specific combining ability	27	0.0144**	0.0052**	0.8106**
Error	1296	0.0005	0.0002	0.0495
Components		X_1	X_2	X_3
$\frac{1}{8}\sum g_i^2$		0.0124[1] (46.10)[2]	0.0242 (82.31)	0.2830 (25.88)
$\frac{1}{27}\sum\sum_{i<j} s_{ij}^2$		0.0140 (52.04)	0.0050 (17.01)	0.7611 (69.60)
$\hat{\sigma}_e^2$		0.0005 (1.86)	0.0002 (0.68)	0.0495 (4.52)

**P<0.01

1) Estimates of the component.

2) Percent value obtained by the component.

TABLE IX. COMBINING ABILITY MEAN SQUARES AND ESTIMATED VARIANCE COMPONENTS, BASED ON MODEL I, FOR SHANK LENGTH(X_4), EAR DIAMETER(X_5), COB DIAMETER(X_6), AND KERNEL DEPTH(X_7) OF JUNE PLANTING

Source	D.F.	Mean Squares			
		X_4	X_5	X_6	X_7
General combining ability	8	7.3528**	0.1545**	0.0709**	0.0056**
Specific combining ability	27	1.8583**	0.0306**	0.0095**	0.0024**
Error	648	0.5646	0.0017	0.0008	0.0003
Components		X_4	X_5	X_6	X_7
$\frac{1}{8}\sum_i g_i^2$		0.9697[1] (34.29)[2]	0.0218 (41.52)	0.0100 (51.28)	0.0008 (25.00)
$\frac{1}{27}\sum\sum_{i<j} s_{ij}^2$		1.2937 (45.75)	0.0290 (55.24)	0.0087 (44.62)	0.0021 (65.63)
$\hat{\sigma}_e^2$		0.5646 (19.96)	0.0017 (3.24)	0.0008 (3.10)	0.0003 (9.37)

**P<0.01

1) Estimates of the component.

2) Percent value obtained by the component.

49.51 per cent, 72.52 per cent, and 21.94 per cent of the variation, respectively, estimated s.c.a. components accounted for 48.86 per cent, 25.56 per cent, and 67.75 per cent of the variation, respectively, and uncontrollable variation accounted for 1.63 per cent, 1.92 per cent, and 10.31 per cent, respectively.

For June planting (Table VII) general and specific combining ability for plant height, ear height, and ear length were significant except for the s.c.a. estimate for plant height. Estimated g.c.a. components for the 3 traits plant height, ear height, and ear length accounted for 24.59 per cent, 79.94 per cent, and 34.00 per cent of the variation, respectively; estimated s.c.a. components accounted for 16.12 per cent, 18.83 per cent, and 61.19 per cent of the variation, respectively, and uncontrollable variation accounted for 59.29 per cent, 1.23 per cent, and 4.81 per cent, respectively.

When both plantings were combined (Table VIII) significant differences were found for both general and specific combining ability. Estimated g.c.a. components for the 3 traits plant height, ear height, and ear length accounted for 46.10 per cent, 82.31 per cent, and 25.88 per cent of the variation, respectively; estimated s.c.a. components accounted for 52.04 per cent, 17.01 per cent, and 69.60 per cent, respectively; and uncontrollable variation accounted for 1.86 per cent, 0.68 per cent, and 4.52 per cent, respectively.

For June planting (Table IX) general and specific combining ability for shank length, ear diameter, cob diameter, and kernel depth were significant. Estimated g.c.a. components for the 4 traits shank length, ear diameter, cob diameter, and kernel depth accounted for

34.29 per cent, 41.52 per cent, 51.28 per cent, and 25.00 per cent, of the variation, respectively; estimated s.c.a. components accounted for 45.75 per cent, 55.24 per cent, 44.62 per cent, and 65.63 per cent of the variation, respectively; and uncontrollable variation accounted for 19.96 per cent, 3.24 per cent, 3.10 per cent, and 9.37 per cent, respectively.

Mean squares obtained from combining ability analyses, based on model II, for the 3 traits plant height, ear height, and ear length of April and June planting and Combined dates are presented in Table X. Variation due to g.c.a. and that due to s.c.a. were significant for all the traits except for plant height of Combined date. Mean squares obtained from combining ability analyses, based on model II, for the 6 traits shank length, ear diameter, cob diameter, kernel depth, weight with husk, weight husked, and mid-silking date of June planting are presented in lower part of Table X. Variation due to g.c.a. and that due to s.c.a. were significant for all the traits except for s.c.a. of shank length and cob diameter.

Additive and Non-additive genetic variance

Estimates of additive genetic, non-additive genetic, total genotypic, environmental, and total phenotypic variance and their standard errors and heritabilities, based on model II, for April and June planting and Combined dates are presented in Table XI. Additive genetic variance estimates were, with the exception of ear length, a major portion of the genotypic variance for each of the traits measured. Estimates of non-additive genetic variance of plant height

TABLE X. MEAN SQUARES FROM COMBINING ABILITY ANALYSES, BASED ON MODEL II, FOR PLANT HEIGHT(X_1), EAR HEIGHT(X_2), EAR LENGTH(X_3), SHANK LENGTH(X_4), EAR DIAMETER(X_5), COB DIAMETER(X_6), KERNEL DEPTH(X_7), WEIGHT WITH HUSK(X_8), WEIGHT HUSKED(X_9), AND MID-SILKING DATE(X_{10}) OF APRIL AND JUNE PLANTING AND COMBINED DATES

Source	D.F.	Mean Squares		
		X_1	X_2	X_3
			April	
General combining ability	8	0.1066**	0.1594**	2.1451*
Specific combining ability	27	0.0155**	0.0085*	1.0216*
Error	35	0.0043	0.0023	0.4785
			June	
General combining ability	8	0.0845**	0.1817**	3.1974**
Specific combining ability	27	0.0275	0.0065**	0.8690**
Error	35	0.0224	0.0021	0.1722
			Combined	
General combining ability	8	0.0874**	0.1693**	2.0304*
Specific combining ability	27	0.0144**	0.0052**	0.8106**
Error	35	0.0066	0.0013	0.1920
			June	
		X_4	X_5	X_6
General combining ability	8	7.3528**	0.1545**	0.0709**
Specific combining ability	27	1.8584	0.0306**	0.0095
Error	35	1.9108	0.0036	0.0055
		X_7	X_8	X_9	X_{10}
General combining ability	8	0.0056*	0.5017**	0.1804**	14.6785**
Specific combining ability	27	0.0024**	0.1028**	0.0555**	3.0859**
Error	35	0.0007	0.0006	0.0006	0.0005

*P<0.05

**P<0.01

TABLE XI. ESTIMATES OF ADDITIVE GENETIC($\hat{\sigma}_A^2$), NON-ADDITIVE GENETIC($\hat{\sigma}_D^2$), TOTAL GENOTYPIC($\hat{\sigma}_G^2$), ENVIRONMENTAL($\hat{\sigma}_e^2$), AND TOTAL PHENOTYPIC($\hat{\sigma}_p^2$) VARIANCES AND THEIR STANDARD ERRORS AND HERITABILITIES($h^2\%$), BASED ON MODEL II, FOR APRIL AND JUNE PLANTING AND COMBINED DATES

Agronomic Trait	Date	$\hat{\sigma}_A^2$	$\hat{\sigma}_D^2$	$\hat{\sigma}_G^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_p^2$	$h^2\%$
Plant height	A	.0260 ± .0153	.0113 ± .0044	.0373 ± .0159	.0110 ± .0006	.0483 ± .0159	77.2
	J	.0163 ± .0123	.0051 ± .0092	.0214 ± .0153	.4330 ± .0241	.4544 ± .0285	4.7
	A+J	.0209 ± .0125	.0078 ± .0040	.0286 ± .0132	.2200 ± .0086	.2486 ± .0158	11.5
Ear height	A	.0431 ± .0228	.0062 ± .0024	.0493 ± .0229	.0120 ± .0007	.0613 ± .0229	80.4
	J	.0501 ± .0260	.0044 ± .0019	.0545 ± .0260	.0080 ± .0004	.0625 ± .0260	87.2
	A+J	.0469 ± .0242	.0040 ± .0014	.0508 ± .0242	.0100 ± .0004	.0608 ± .0242	83.5
Ear length	A	.3210 ± .3166	.5431 ± .3007	.8641 ± .4366	2.6950 ± .1497	3.5591 ± .4616	24.2
	J	.6652 ± .4618	.6968 ± .2401	1.3621 ± .5204	1.2670 ± .0704	2.6291 ± .5252	51.8
	A+J	.3485 ± .2968	.6186 ± .2222	.9671 ± .3708	1.9800 ± .0778	2.9471 ± .3789	32.8

A = April, J = June, A+J = Combined April & June

for June planting were relatively small quantities. As indicated by the magnitude of their standard errors, these estimates of variance are subjected to considerable sampling errors (38,55).

The estimates of genotypic variance were a major portion of the phenotypic variance for the April planting and Combined dates, but the estimates of environmental variance were a major portion of the phenotypic variance for June planting of plant height. For ear height, the estimates of genotypic variance were a major portion of the phenotypic variance. In contrast, ear length was generally affected by the environmental variance.

Heritability in the broad sense was calculated by the method using the notation of Allard (1).

$$(\hat{h}^2 = \hat{\sigma}_g^2/\hat{\sigma}_p^2)$$

For plant height in April planting, the estimated heritability in the broad sense was 77.2 per cent of the observed phenotypic variance, which implies that in the F_1 generation 77.2 per cent was due to genetic causes (additivity, dominance and interactions) and that 22.8 per cent of the total variance was environmental in origin. However for plant height in the June planting, the estimated heritability was 4.7 per cent. Thus, in the F_1 generation, only 4.7 per cent of the total variance was due to genetic causes, and 95.3 per cent was environmental in origin. This great discrepancy of heritability percentage between April and June planting can be partially explained by the late mosaic in the June planting. For ear height in April and June planting and Combined dates, the estimated heritabilities were 80.4 per cent, 87.2 per cent, and

83.5 per cent, respectively, which implies that in the F_1 generation fairly high percentage were due to genetic causes. In contrast, ear length in April and June planting and Combined dates, the estimated heritabilities were 24.2 per cent, 51.8 per cent, and 32.8 per cent, respectively, which implies that fairly low percentage was due to genetic causes.

Estimates of additive genetic, non-additive genetic, total genotypic, environmental, and total phenotypic variances and their standard errors and heritabilities, based on model II, for June planting are presented in Table XII.

The estimates of additive genetic variance were a major portion of the genotypic variance for each of the traits measured. Two exceptions to this pattern occurred in kernel depth and weight without husk. The estimates of non-additive genetic variance of shank length were negative quantities. These estimates of variances are subjected to considerable sampling error (38,55). The estimates of genotypic variance were a major portion of the phenotypic variance for each of the traits measured except for the shank length and kernel depth.

The estimated heritabilities of weight with husk, weight without husk, and mid-silking were 97.7 per cent, 94.7 per cent, and 99.9 per cent, respectively, which implies that in the F_1 generation quite high percentages of the observed phenotypic variances were due to genetic causes. However the estimated heritabilities of shank length, ear diameter, cob diameter, and kernel depth were 11.8 per cent, 65.4 per cent, 55.8 per cent, and 30.2 per cent, respectively, which implies that in the F_1 generation relatively low percentages of the observed phenotypic

TABLE XII. ESTIMATES OF ADDITIVE GENETIC($\hat{\sigma}_A^2$), NON-ADDITIVE GENETIC($\hat{\sigma}_D^2$), TOTAL GENOTYPIC($\hat{\sigma}_G^2$), ENVIRONMENTAL($\hat{\sigma}_e^2$), AND TOTAL PHENOTYPIC($\hat{\sigma}_p^2$), VARIANCES AND THEIR STANDARD ERRORS AND HERITABILITIES(h^2%), BASED ON MODEL II, FOR JUNE PLANTING

Agronomic Trait	$\hat{\sigma}_A^2$	$\hat{\sigma}_D^2$	$\hat{\sigma}_G^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_p^2$	h^2%
Plant height	.0163± .0123	.0051± .0092	.0214± .0153	.4330± .0241	.4544± .0285	4.7
Ear height	.0501± .0260	.0044± .0019	.0545± .0260	.0080± .0004	.0625± .0260	87.2
Ear length	.6652± .4618	.6968± .2401	1.3621± .5204	1.2670± .0704	2.6291± .5252	51.8
Shank length	1.5699±1.0603	-.0525± .6815	1.5174±1.2604	11.2920± .6273	12.8094±1.4079	11.8
Ear diameter	.0354± .0222	.0270± .0084	.0624± .0237	.0330± .0018	.0954± .0238	65.4
Cob diameter	.0176± .0102	.0040± .0029	.0215± .0106	.0170± .0009	.0385± .0106	55.8
Kernel depth	.0009± .0008	.0017± .0007	.0026± .0011	.0060± .0003	.0086± .0011	30.2
Weight with husk	.1140± .0721	.1022± .0280	.2162± .0774	.0050± .0003	.2212± .0774	97.7
Weight without husk	.0357± .0261	.0549± .0151	.0906± .0302	.0050± .0003	.0956± .0320	94.7
Mid-silking	3.3122±2.1106	3.0854± .8399	6.3976±2.2716	.0050± .0003	6.4026±2.2716	99.9

variances were due to genetic causes.

General Combining Ability Effects of Individual Parents

Estimates of general combining ability effects of 9 parents for April and June planting and Combined dates are presented in Tables XIII and XIV. The estimates of g.c.a. effects revealed wide differences between the mainland inbreds and Hawaiian inbreds for all the traits. This would indicate that there is considerable scope for improvement of each trait.

Plant height:

Parents AA18, AA8, AA11 and AA20 showed high g.c.a. effects for greater plant height in the April planting (Table XIII), indicating that these parents are good general combiners and may be expected to produce tall hybrids. The three shortest parents, 190a, 2277, and P39 had a highly significant negative g.c.a. effects, indicating that these parents may be expected to produce short hybrids.

Parents AA18, AA8, AA20 and AA11 showed high g.c.a. effects for greater plant height in Combined dates (Table XIII), indicating that these parents are good general combiners and may be expected to produce tall hybrids. The three shortest parents, 190a, 2277, and P39 had a highly significant negative g.c.a. effects, indicating that these parents may be expected to produce short hybrids.

Parents AA18, AA8 and AA11 showed high g.c.a. effects for greater plant height in June planting (Table XIV), indicating that these parents are good general combiners and may be expected to produce tall hybrids.

TABLE XIII. ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS FOR PLANT HEIGHT($\hat{1g}_i$), EAR HEIGHT($\hat{2g}_i$), AND EAR LENGTH($\hat{3g}_i$) OF APRIL PLANTING AND COMBINED DATES

Parent	General Combining Ability Effects					
	April			Combined		
	$\hat{1g}_i$	$\hat{2g}_i$	$\hat{3g}_i$	$\hat{1g}_i$	$\hat{2g}_i$	$\hat{3g}_i$
AA8	0.121	0.122	-0.535	0.104	0.116	-0.480
AA11	0.081	0.121	-0.032	0.103	0.135	0.010
AA18	0.143	0.203	-0.679	0.134	0.201	-0.160
AA20	0.074	0.151	0.632	0.071	0.167	0.525
190a	-0.182	-0.203	0.867	-0.169	-0.183	0.746
245	0.058	-0.034	-0.135	0.012	-0.027	0.253
2277	-0.131	-0.121	-0.329	-0.127	-0.152	-0.532
P39	-0.138	-0.149	-0.342	-0.093	-0.165	-0.820
T19	-0.027	-0.091	0.553	-0.035	-0.091	0.457
S.E.($\hat{g}_i - \hat{g}_j$)	0.012	0.013	0.196	0.039	0.008	0.118

TABLE XIV. ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS FOR THE TRAITS PLANT HEIGHT($_1\hat{g}_i$), EAR HEIGHT($_2\hat{g}_i$), EAR LENGTH($_3\hat{g}_i$), SHANK LENGTH($_4\hat{g}_i$), EAR DIAMETER($_5\hat{g}_i$), COB DIAMETER($_6\hat{g}_i$), AND KERNEL DEPTH($_7\hat{g}_i$) OF JUNE PLANTING

Parent	General Combining Ability Effects						
	$\hat{g}_{1i}$	$\hat{g}_{2i}$	$\hat{g}_{3i}$	$\hat{g}_{4i}$	$\hat{g}_{5i}$	$\hat{g}_{6i}$	$\hat{g}_{7i}$
AA8	0.090	0.115	-0.424	-1.321	-0.047	-0.050	-0.024
AA11	0.127	0.155	0.056	-0.571	0.001	-0.075	0.029
AA18	0.128	0.176	0.358	-0.885	0.058	0.036	-0.007
AA20	0.078	0.189	0.418	-0.852	0.159	0.083	0.027
190a	-0.173	-0.185	0.623	-0.252	0.239	0.220	0.024
245	-0.031	-0.014	0.640	0.653	0.074	-0.005	0.030
2277	-0.112	-0.176	-0.736	0.553	-0.207	-0.102	-0.037
P39	-0.046	-0.174	-1.301	1.808	-0.118	-0.050	-0.005
T19	-0.061	-0.085	0.364	0.867	-0.158	-0.055	-0.035
S.E.($\hat{g}_i - \hat{g}_j$)	0.078	0.010	0.134	0.401	0.021	0.015	0.009

Parents 190a and 2277 had highly significant negative g.c.a. effects, indicating that these parents may be expected to produce short hybrids.

Ear height:

Parents AA18, AA20, AA11, and AA8 showed highly significant g.c.a. effects for greater ear height in the April planting (Table XIII), indicating that these parents are good general combiners and may be expected to increase ear height, whereas parents 190a, P39, 2277, T19, and 245 may be expected to decrease ear height.

Parents AA20, AA18, AA11, and AA8 showed highly significant g.c.a. effects for greater ear height in the June planting (Table XIV), indicating that these parents are good general combiners and may be expected to increase ear height, whereas parents 190a, P39, 2277, and T19 may be expected to decrease ear height.

When both plantings were combined (Table XIII), parents AA18, AA20, AA11, and AA8 showed highly significant g.c.a. effects, indicating these parents are good general combiners and may be expected to increase ear height, whereas parents 190a, P39, 2277, T19, and 245 may be expected to decrease ear height.

Ear length:

Parents AA20, 190a, and T19 showed highly significant g.c.a. effects for ear length in the April planting (Table XIII), indicating that these parents are good general combiners and may be expected to increase ear length, whereas parents AA18, AA8, P39, and 2277 may be expected to decrease ear length.

Parents AA20, 190a, AA18, 245, and T19 showed highly significant g.c.a. effects for greater ear length in the June planting (Table XIV), indicating that these parents are good general combiners and may be expected to decrease ear length.

When both plantings were combined (Table XIII), parents 190a, AA20, T19, and 245 showed highly significant g.c.a. effects, indicating that these parents are good general combiners and may be expected to increase ear length, whereas parents P39, 2277, and AA8 may be expected to decrease ear length.

Shank length:

Parents P39 and T19 had significant g.c.a. effects, indicating that these parents are good general combiners and may be expected to increase shank length, whereas parents AA8, AA18, and AA20 may be expected to decrease shank length.

Ear diameter:

Parents 190a, AA20, and AA18 showed highly significant g.c.a. effects for greater ear diameter, indicating that these parents are good general combiners and may be expected to increase ear diameter, whereas 2277, T19, P39, and AA8 may be expected to decrease ear diameter.

Cob diameter:

Parents 190a, AA20, and AA18 showed highly significant g.c.a. effects for greater cob diameter, indicating that these parents are good general combiners and may be expected to increase cob diameter, whereas

parents 2277, AA11, T19, AA8, and P39 may be expected to decrease cob diameter.

Kernel depth:

Parents AA11, AA20, 190a, and 245 showed highly significant g.c.a. effects for kernel depth, indicating that these parents are good general combiners and may be expected to increase kernel depth, whereas parents AA8, 2277, and T19 may be expected to decrease kernel depth.

Specific Combining Ability Effects

Estimates of general and specific combining ability effects and variances for plant height of each planting date and associated standard errors are presented in Table XV. Specific combining ability effects represent the deviations of an individual single cross from the general combining ability effects. The estimated s.c.a. effects of series of AA crosses were shorter than would be expected on the basis of the average cross performance of the parent inbreds.

Parents like AA18 generally produced very tall hybrids, and the associated g.c.a. effect value was highly significant. One exception to this pattern occurred in the cross AA18 x AA20. These inbreds were closely related so their hybrids were shorter than would be expected on the basis of g.c.a. values. This reduction in height was reflected in the very large negative values for the s.c.a. effect for this hybrid. This appears also to have been reflected in the small s.c.a. variance for parents AA18 and AA20.

TABLE XV. ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITY EFFECTS AND THEIR ASSOCIATED VARIANCES AND CORRESPONDING STANDARD ERRORS FOR PLANT HEIGHT OF EACH PLANTING DATE

Parent	Date	Parent (S.C.A. effects)								G.C.A. effects	G.C.A. & S.C.A. variance	
		AA11	AA18	AA20	190a	245	2277	P39	T19	$\hat{g}_i$	$\hat{\sigma}^2_{g_i}$	$\hat{\sigma}^2_{s_i}$
AA8	A	-.025	-.127	-.044	.029	.055	.075	.051	-.015	.121	.014	.004
	J	.012	.001	-.020	.017	.087	-.130	-.023	.050	.090	.005	-.014
	A+J	-.005	-.061	-.006	-.002	.073	-.022	.015	.008	.104	.010	-.003
AA11	A		.036	-.079	-.038	.124	-.021	-.026	.030	.081	.006	.003
	J		.004	-.085	.190	.087	-.110	-.196	.098	.127	.013	-.002
	A+J		.021	-.077	.067	.107	-.060	-.109	.056	.103	.010	.001
AA18	A			-.390	.061	.065	.119	.190	.045	.143	.020	.032
	J			-.202	.051	.060	-.048	.058	.075	.128	.013	-.010
	A+J			-.291	.048	.064	.041	.126	.052	.134	.017	.011
AA20	A				.093	.118	.106	.128	.068	.074	.005	.030
	J				.018	.103	-.015	.031	.127	.078	.003	-.007
	A+J				.050	.116	.027	.085	.094	.071	.004	.013
190a	A					.011	.004	-.178	.018	-.182	.033	.006
	J					-.042	-.078	-.153	.032	-.173	.027	-.008
	A+J					-.024	-.041	-.174	.076	-.169	.028	.002
245	A						-.154	-.148	-.071	.058	.003	.012
	J						-.104	-.143	-.048	-.031	-.001	.009
	A+J						-.124	-.144	-.068	.012	-.001	.006
2277	A							-.035	-.095	-.131	.017	.008
	J							.074	-.136	-.112	.009	.046
	A+J							.021	-.120	-.127	.015	.013
P39	A								.018	-.138	.019	.015
	J								-.199	-.046	-.001	.055
	A+J								-.099	-.093	.008	.022
T19	A									-.027	.001	.003
	J									-.061	.001	.005
	A+J									-.035	.001	.002

Standard error	April	June	A+J
S.E. $(\hat{s}_{ij} - \hat{s}_{ik})$	0.030	0.192	0.097
S.E. $(\hat{s}_{ij} - \hat{s}_{kl})$	0.028	0.175	0.088

The greatest s.c.a. effects to increase plant height were found in the crosses AA11 x 245, AA18 x P39, AA20 x 245, AA20 x P39, and AA20 x T19. In contrast 190a, 2277, and P39 proved to be superior parents for reducing plant height, as indicated by their high negative g.c.a. values. There did not appear to be significant non-additive variance associated with reduction in height, as indicated by the small s.c.a. variance associated with parents 190a, 2277, and P39. The greatest reductions in plant height were found in crosses of AA20 with AA8, AA11, and AA18; in crosses 245 with 2277, P39, and T19, and in crosses of AA11 with 2277 and P39.

Estimates of general and specific combining ability effects and their associated variances and the corresponding standard errors for ear height of each planting date are presented in Table XVI.

Parents like AA8, AA11, AA18, and AA20 generally increased ear height, and the associated g.c.a. effect value was highly significant. But the estimated s.c.a. effects of a series of AA crosses were shorter than would be expected on the basis of the average cross performance of the parents. This reduction in ear height was reflected in the very large negative values for the s.c.a. effect for this hybrid. This appears also to have been reflected in the small s.c.a. effect for these parents. The greatest reduction in ear height were found in crosses of AA8 with P39 and T19; in crosses of AA11 with 2277 and P39, and in crosses of 245 with 2277, P39 and T19.

Parents like 190a, P39, and 2277 proved to be superior parents for reducing ear height, as indicated by their high negative g.c.a. effect values. There did not appear to be significant non-additive variance

TABLE XVI. ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITY EFFECTS AND THEIR ASSOCIATED VARIANCES AND THE CORRESPONDING STANDARD ERRORS FOR EAR HEIGHT OF EACH PLANTING DATE

Parent	Date	Parent (S.C.A. effects)								G.C.A. effects	G.C.A. & S.C.A. variance	
		AA11	AA18	AA20	190a	245	2277	P39	T19	$2\hat{g}_i$	$\hat{\sigma}g_i^2$	$\hat{\sigma}s_i^2$
	A	.028	-.122	-.019	.059	.020	.044	.022	-.033	.122	.015	.003
AA8	J	-.047	.009	-.041	.050	.046	-.050	.073	-.040	.115	.013	.002
	A+J	-.005	-.066	-.027	.043	.036	.001	.051	-.033	.116	.013	.001
	A		.044	.005	-.009	.006	-.046	-.090	.060	.121	.015	.002
AA11	J		-.003	-.086	.177	-.002	-.014	-.062	.039	.155	.024	.006
	A+J		.010	-.037	.073	.005	-.027	-.072	.053	.135	.018	.002
	A			-.294	.023	.094	.071	.120	.062	.203	.042	.019
AA18	J			-.107	-.162	.058	-.051	.121	.135	.176	.031	.011
	A+J			-.212	.005	.065	-.001	.110	.088	.201	.041	.010
	A				.004	.105	.032	.124	.041	.151	.023	.016
AA20	J				.027	.076	.071	.022	.039	.189	.036	.005
	A+J				.005	.094	.056	.077	.043	.167	.028	.009
	A					-.024	-.002	-.080	.029	-.203	.041	.001
190a	J					-.074	.014	-.011	-.021	-.185	.034	.009
	A+J					-.059	-.005	-.056	-.006	-.183	.033	.002
	A						-.113	-.073	-.015	-.034	.001	.005
245	J						.015	-.063	-.056	-.014	.001	.003
	A+J						-.044	-.065	-.032	-.027	.001	.003
	A							.067	-.053	-.121	.014	.004
2277	J							.015	-.001	-.176	.031	.001
	A+J							.044	-.023	-.152	.023	.001
	A								.018	-.149	.022	.009
P39	J								-.094	-.174	.030	.005
	A+J								-.205	-.165	.027	.006
	A									.013	.008	.003
TI9	J									-.085	.007	.005
	A+J									.008	.008	.010

Standard error	April	June	A+J
S.E. $(\hat{s}_{ij} - \hat{s}_{ik})$	0.032	0.026	0.020
S.E. $(\hat{s}_{ij} - \hat{s}_{kl})$	0.029	0.023	0.018

associated with reduction in ear height, as indicated by the small s.c.a. variance associated with parents 190a, P39, and 2277. One exception occurred in the crosses of 245 with 2277, P39, and T19. These specific combinations appear to be due to significant non-additive variance. The greatest effects to reduce ear height were found in crosses of AA8 with P39 and T19, in crosses of AA8 with 2277 and P39 and in crosses of 245 with 2277, P39, and T19. These specific combinations give ear height shorter than expected on the basis of the average cross performance of the parent.

Estimates of general and specific combining ability effects and their associated variances and the corresponding standard errors for ear length for April and June planting and combined dates are presented in Table XVII.

Parents like AA20, 190a, and T19 generally produced greater ear length, and the associated g.c.a. effect value was highly significant. But the estimated s.c.a. effect in crosses of AA20 with either AA11, or AA18, of 190a with either P39 or T19, and of T19 with either 245, 2277 or P39 were shorter than would be expected on the basis of the average cross performance of the parents. This reduction in ear length was reflected in the very large negative values for the s.c.a. effect for these hybrids. The greatest s.c.a. effects for increased ear length were found in crosses of AA8 with either AA20, P39, or T19, of AA11 with either 190a, or P39, of AA18 with either 190a, P39 or T19, of AA20 with either 245 or T19 and of 2277 with either P39 or 245, which indicated that specific combinations give ear length longer than expected on the basis of the average cross performance of the parent.

TABLE XVII. ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITY EFFECTS AND THEIR ASSOCIATED VARIANCES AND THE CORRESPONDING STANDARD ERRORS FOR EAR LENGTH OF EACH PLANTING DATE

Parent	Date	Parent (S.C.A. effects)								G.C.A. effects	G.C.A. & S.C.A. variance	
		AA11	AA18	AA20	190a	245	2277	P39	T19	$\hat{g}_{i1}$	$\hat{\sigma}^2_{g_i}$	$\hat{\sigma}^2_{s_i}$
AA8	A	-.432	-.035	.283	.697	-.145	-.735	-.092	.462	-.535	.269	.104
	J	.678	-.024	.415	-.768	-.406	-.208	.705	-.390	-.424	.171	.243
	A+J	.121	-.026	.347	-.033	-.281	-.465	.303	.034	-.480	.224	.032
AA11	A		-.037	-.269	.615	.917	-.507	.355	-.640	-.032	-.016	.209
	J		-.954	-.464	.731	-.186	-.288	.275	.209	.056	-.005	.283
	A+J		-.498	-.363	.674	.367	-.396	.311	-.216	.010	-.006	.141
AA18	A			-3.022	.242	-.085	-.160	1.722	1.376	-.679	.444	1.897
	J			-2.697	1.348	.781	-.561	1.072	1.036	.358	.120	1.825
	A+J			-2.862	.796	.348	-.365	1.403	1.204	-.160	.019	1.779
AA20	A				.580	.653	.247	.760	.765	.632	.382	1.495
	J				.168	1.221	.088	.192	1.076	.418	.167	1.429
	A+J				.370	.943	.168	.477	.918	.525	.269	1.468
190a	A					-.542	.792	-1.475	-.910	.867	.735	.625
	J					.066	.173	-.641	-1.077	.623	.380	.599
	A+J					-.238	.477	-1.053	-.992	.746	.551	.473
245	A						.815	-1.542	-.067	-.135	.001	.547
	J						.606	-1.408	-.674	.640	.402	.676
	A+J						.710	-1.481	-.369	.253	.058	.545
2277	A							.402	-.853	-.329	.091	.322
	J							.088	.102	-.736	.534	.069
	A+J							.244	-.373	-.532	.276	.167
P39	A								-.130	-.342	.100	1.086
	J								-.283	-1.301	1.684	.522
	A+J								-.205	.820	.667	.785
T19	A									.553	.289	.553
	J									.364	.124	.536
	A+J									.457	.203	.478

Standard error	April	June	A+J
S.E. $(\hat{s}_{ij} - \hat{s}_{ik})$	0.480	0.329	0.291
S.E. $(\hat{s}_{ij} - \hat{s}_{kl})$	0.438	0.300	0.265

Estimates of general and specific combining ability effects and their associated variances and the corresponding standard errors for shank length, ear diameter, cob diameter, and kernel depth of June planting, are presented in Table XVIII.

Shank length:

The largest s.c.a. effects for increased shank length were found in crosses of AA8 with either 2277, T19, P39, AA18 or AA11, of AA11 with either AA20, 245 or T19, of AA18 with either 245, 190a or P39, of AA20 with either 245, T19 or 2277, of 190a with either T19 or 2277, and of 245 with P39, which indicated that specific combinations give shank length longer than expected on the basis of the average cross performance of the parent. In contrast the greatest s.c.a. effects for decreased shank length were found in crosses of AA11 with either AA18 or 190a, of AA20 with either AA8 or AA18, of 190a with either 245 or P39, of 245 with either 2277 or T19 and of T19 with either 2277 or P39, which indicated that specific combinations give shank length shorter than expected on the basis of the average cross performance of the parents.

Ear diameter:

The greatest s.c.a. effects for increased ear diameter were found in crosses of AA8 with either 245 or P39, of AA11 with either 190a, T19 or 245, of AA18 with either 190a, P39 or T19, and of AA20 with 2277, which indicated that specific combinations give ear diameters larger than expected on the basis of the average cross performance of the parent. In contrast the greatest s.c.a. effects for decreased ear

TABLE XVIII. ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITY EFFECTS AND THEIR ASSOCIATED VARIANCES AND THE CORRESPONDING STANDARD ERRORS FOR SHANK LENGTH(X_4), EAR DIAMETER(X_5), COB DIAMETER(X_6), AND KERNEL DEPTH(X_7) OF JUNE PLANTING

Parent	Traits	Parent (S.C.A. effects)								G.C.A. effects	G.C.A. & S.C.A. variance	
		AA11	AA18	AA20	190a	245	2277	P39	T19	$\hat{g}_i$	$\hat{\sigma}g_i^2$	$\hat{\sigma}s_i^2$
	X_4	.142	.216	-2.696	-.986	-.691	2.118	.282	1.613	-1.321	1.673	1.795
	X_5	-.019	-.122	-.118	-.118	.211	-.026	.069	-.065	-.047	.002	.011
AA8	X_6	.090	-.072	-.125	-.125	.080	.031	-.009	-.085	-.050	.003	.004
	X_7	-.020	-.024	.037	-.025	.039	-.003	.015	-.020	-.024	.001	.001
	X_4		-1.553	1.053	-.706	.368	.228	.122	.343	-.571	.254	.139
	X_5		-.201	-.022	.398	.037	.030	.026	.051	.001	-.000	.007
AA11	X_6		-.067	.025	-.030	.105	-.078	.020	-.065	-.075	.006	.004
	X_7		-.068	-.052	.051	.030	.048	.011	.001	.029	.001	.002
	X_4			-1.531	1.208	1.362	.052	.506	-.261	-.885	.712	.723
	X_5			-.525	.355	.039	.067	.198	.188	.058	.003	.076
AA18	X_6			-.201	.152	-.002	.089	-.007	.107	.036	.001	.013
	X_7			-.121	.092	.031	-.001	.052	.037	-.007	.000	.005
	X_4				-.674	2.049	1.019	-.486	1.265	-.852	.655	2.125
	X_5				.073	.043	.231	.076	.051	.159	.025	.049
AA20	X_6				.090	.005	.012	-.014	.009	.083	.007	.008
	X_7				.018	.047	.055	-.017	.033	.027	.001	.003
	X_4					-.410	.219	-.396	1.745	-.252	-.008	.488
	X_5					-.061	-.068	-.277	-.002	.239	.057	.033
190a	X_6					-.035	.080	-.080	-.051	.220	.048	.009
	X_7					-.035	-.022	-.049	-.023	.024	.001	.002
	X_4						-1.736	1.268	-2.210	.653	.355	1.852
	X_5						-.073	-.048	-.148	.074	.005	.010
245	X_6						-.018	-.054	-.080	-.005	-.000	.003
	X_7						-.043	-.025	-.045	.030	.001	.001
	X_4							.351	-1.550	.553	.234	1.112
	X_5							-.065	-.095	-.207	.043	.010
2277	X_6							-.078	-.039	-.102	.010	.004
	X_7							-.022	-.012	-.037	.001	.001
	X_4								-.946	1.808	3.200	-.002
	X_5								.020	-.118	.014	.018
P39	X_6								.224	-.050	.003	.009
	X_7								.036	-.005	-.000	.001
	X_4									.867	.681	1.748
	X_5									-.158	.025	.010
T19	X_6									-.055	.003	.011
	X_7									-.035	.001	.001

Standard error	X_4	X_5	X_6	X_7
S.E. $(\hat{S}_{ij} - \hat{S}_{ik})$	0.983	0.053	0.038	0.023
S.E. $(\hat{S}_{ij} - \hat{S}_{kl})$	0.898	0.048	0.034	0.021

diameter were found in crosses of AA8 with either AA18, AA20 or 190a, of AA11 with either AA18 or AA20, of AA18 with AA20, of AA20 with either 245 or T19, of 190a with either P39, 2277 or 245, and of 245 with either T19, 2277 or P39, which indicated that specific combinations give ear diameters smaller than expected on the basis of the average cross performance of the parent.

Cob diameter:

The greatest s.c.a. effect for increased cob diameter were found in crosses of AA8 with either AA11, T19 or 245, of AA11 with either 245, 2277 or AA20, of AA18 with either 190a, T19 or 2277, and of P39 with T19, which indicated that specific combinations give cob diameter longer than expected on the basis of the average cross performance of the parent. In contrast the greatest s.c.a. effects for decreased cob diameter were found in crosses of AA8 with either AA20, 190a or AA11, of AA18 with either AA20, P39 or 245, of AA20 with P39, of 190a with either 2277, P39 or T19, and of 245 with either T19, P39 or 2277, which indicated that specific combinations give cob diameter smaller than expected on the basis of the average cross performance of the parents.

Kernel depth:

The greatest s.c.a. effects for increased kernel depth were found in crosses of AA8 with either 245, AA20 or P39, AA11 with either 190a or 2277, of AA18 with either 190a, P39 or T19, of AA20 with either 2277 or 245, and of P39 with T19, which indicated that specific combinations give kernel depths larger than expected on the basis of the average

cross performance of the parent. In contrast the greatest s.c.a. effects for reduced kernel depth were found in crosses of AA11 with either AA18 or AA20, of AA20 with either AA18 or P39, of 190a with either P39, 245 or T19, and of 245 with either T19, 2277 or P39, which indicated that specific combinations give kernel depth shorter than expected on the basis of the average cross performance of the parents.

DISCUSSION

All of the genetic models used in the study of quantitative inheritance have involved certain assumptions in order to simplify statistical procedures. Some of the assumptions are more important than others in causing bias in the estimates of gene effects. Anderson and Kempthorne (2) used the following assumptions in the development of their genetic model: 1) multiple alleles absent; 2) linkage absent; 3) lethal gene absent; 4) constant viability for all genotypes; 5) environmental effects additive with the genotypic value.

There would be no serious bias expected in the estimates of the parameters from assumptions 1), 3), and 4). Since the populations used in this study are presumably homozygous lines, multiple alleles would be present only if the parental lines were not homozygous or if mutation occurred. Lethal genes are not likely to be present in the crosses since the parental inbred lines used in the study have been maintained by selfing for many generations. Viability, perhaps, is not constant for all genotypes but was satisfactory in the tests conducted and negligible bias would be expected.

The assumption that presence of linkage and environmental effects are non-additive with the genotypic value is not applicable to the materials under study.

Robinson, et al. (55), Robinson and Comstock (56), and Williams, et al. (64) discussed the implications of the ratio $\hat{\sigma}_D^2/\hat{\sigma}_A^2$ relative to the type of gene action involved in the inheritance of quantitative characters. Their implications and underlying assumptions were applicable to the present data. Paralleling the reports of these

authors, the estimates of plant height and ear height indicated partial to complete dominance or a combination of partial dominance and over-dominance. On the other hand, the estimates of ear length indicated high degree of dominance (Table XI). The estimates from June planting indicated partial to complete dominance for ear height, cob diameter, plant height, ear diameter, weight with husk, and mid-silking date. In addition ear length, weight without husk, and kernel depth were influenced by a high degree of dominance (Table XII).

A prominant and disturbing result noted in these data (Table XII) was the preponderance of negative dominance variance obtained in shank length. One possible explanation for these negative estimates was sampling error, i.e. the negative estimates resulted from sampling error in estimating a quantity which is either zero or a small positive value (38,55). The actual existence of negative dominance variance is not in question, since as Robinson, et al. (55) pointed out, variance, by definition is never negative. If sampling error was the only contributing factor, repeated sampling of a variety in which the dominance variance is zero should, on the average, give estimates fluctuating about zero with approximately half of them being positive.

For interpretation of the results presented, it was assumed that differences in general combining ability resulted primarily from differences in the additive effects of genes, and that differences in specific combining ability were due to differences in the non-additive (dominance) effects of genes. Kempthorne (34,35,36) has shown that ignoring epistacy in the estimation of genotypic components places restrictions on the interpretation of any estimates obtained. The model

used in this study did not take epistacy into account, thus biasing the result presented to an unknown extent.

Estimates of the relative importance of general and specific combining ability in the population studied were obtained from comparisons of the variance components. Rojas and Sprague (57) found that variances for specific combining ability effects became of relatively greater importance than the variances for general combining ability effects when the lines under test had been subject to previous testing and selection. The inbred lines used in this study were all highly selected and are used commonly in various hybrid combinations of sweet corn throughout the United States. Therefore one might expect that the specific combining ability portion of the genotypic variance should be expressed to a pronounced extent in the population evaluated.

Additive gene effects appeared to be more important for plant height, ear height, shank length, ear diameter, cob diameter, weight with husk, and mid-silking date. This corresponds to the results of Gamble (12) that additive genetic variation is greater in the traits which are assumed to have a less complex inheritance. Amount of additive variation seems to be sufficient for further improvement of these traits through selection.

In comparing with additive gene effects, dominance gene effects appeared to be more important for ear length, kernel depth, and weight without husk than for other traits. This may suggest, as the inheritance of a quantitative character becomes more complex, the contribution of dominance gene effects to the inheritance becomes greater.

Heritability estimates for plant height, ear height, ear length, shank length, ear diameter, cob diameter, kernel depth, weight with husk, weight without husk, and mid-silking date were 11.5, 83.5, 32.8, 11.8, 65.4, 55.8, 30.2, 97.7, 94.7, and 99.9 per cent, respectively. These estimates support the conclusion that selection for mid-silking date, weight with and without husk, ear height, ear diameter, and cob diameter would be most effective and that selection for plant height, ear length, shank length, and kernel depth would be least effective.

SUMMARY

A diallel set of nine inbred lines of sweet corn and all possible F_1 hybrids, excluding reciprocals were analyzed for combining ability for plant height, ear height, ear length, shank length, ear diameter, cob diameter, kernel depth, weight with husk, weight without husk, and mid-silking date.

Considerable differences for all agronomic traits were observed in a majority of the F_1's with variable degrees of dominance. The analysis for combining ability revealed predominantly additive gene effect for plant height, ear height, shank length, ear diameter, cob diameter, weight with husk, and mid-silking date and mostly non-additive (dominance) gene effect for the other traits.

Heritability estimates support the conclusion that selection for mid-silking date, weight with and without husk, ear height, ear diameter, and cob diameter would be most effective and that selection for plant height, ear length, shank length, and kernel depth would be least effective.

On the basis of general combining ability for all the traits, 190a, and 2277, both mainland inbreds, were the best for reducing plant and ear height, AA20 and 190a were the best inbred for increasing ear length, ear diameter, cob diameter, and kernel depth. The specific combining ability effects indicated that no cross combination was consistently good for all the traits. However, the crosses involving P39, 2277, and T19 have desirable specific combining ability effects when all the combinations are considered together.

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